

Floral and Pollination Biology of Two Gynodioecious Herbs, *Dianthus shinanensis* and *D. superbus* (Caryophyllaceae)

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Dianthus superbus and *D. shinanensis* are common gynodioecious herbs occurring in grasslands and riverbeds in central Honshu of Japan. We investigated the reproductive nature and pollination systems of the two species to determine what differences in reproductive success and pollination might exist between these taxa and between female and hermaphrodite plants, and whether seed production was limited by pollen availability. In *D. superbus* the female plants produced more numerous seeds than the hermaphrodite plants, or produced seeds equal to the hermaphrodite ones in natural populations. Both hermaphrodite and female flowers of the species were largely pollinated by large-sized butterflies and hawkmoths sucking the nectars, and did not differ from each other in frequency of flower visitors. In *D. shinanensis*, on the other hand, the seed set percentages were significantly lower in the female plants than in the hermaphrodite plants. The effective pollinators of the species were mainly middle-sized butterflies sucking the nectars and bees and hover-flies feeding on pollen grains, but the frequency of flower visitors was obviously lower in the female plants than in the hermaphrodite plants. The lower female reproductive success (i.e., seed production) of *D. shinanensis* may be caused by the reduced visits of the insect pollinators due to lacking pollen rewards.

Key words: Caryophyllaceae, *Dianthus*, *D. shinanensis*, *D. superbus*, female plant, gynodioecy, pollination system, reproductive success, seed production

Gynodioecy is the occurrence of hermaphrodite and female plants in natural populations, as defined by Darwin (1877). Sex expression of this type is widely observed in various flowering plants belonging to unrelated genera and families (Bawa & Beach 1981, Uno 1982, Weller & Sakai 1990, Kawakubo 1994, Sugawara & Horii 1995, 1999, Suzuki & Akazome 2000, see also Richards 1997, Eckhart 1999). *Dianthus superbus* L. and *D. shinanensis* (Yatabe) Makino (Caryophyllaceae) are common plants growing in riverbed and grassy plains of mountains in central Honshu of Japan, and they are distinguished from each other in inflorescence architecture and corolla-tube length (Kitagawa 1982). In earlier studies, the

sex expression of the former species was well documented as a gynodioecy (Yahara 1988, Sugawara *et al.* 1994), while that of the latter species is unknown. During our field survey, we found that *D. shinanensis* was also gynodioecious, and that fruit and seed production of *D. shinanensis* appeared to be less in the female plants than in the hermaphrodite ones, while those of *D. superbus* appeared to be not different between the two sexual forms. We wonder how different sexual forms of the two species function in fruit and seed production and in pollination system under natural populations.

In the gynodioecious species, female plants usually lack fertile pollen grains and thereby the plants

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depend on pollen vectors for pollination (Bawa & Beach 1981, Richards 1997). Nevertheless, it is generally known that the female plants produce seeds equal to the hermaphrodite ones, or produce more numerous seeds than the hermaphrodite ones in natural populations (Uno 1982, Delph 1990, Richards 1997, Manicacci *et al.* 1998). For the two *Dianthus* species concerned, information on the reproductive natures is still insufficient. In this paper we investigated the pollination biology and the reproductive nature of the two gynodioecious *Dianthus* species. Our goals are to demonstrate the quantitative data for reproductive success (i.e., seed production) of the two sexual forms in the two gynodioecious *Dianthus* species, to identify pollen vectors of both species and to determine whether the reproductive success is limited by pollen availability between different sexual forms of the species.

Materials and Methods

Study species and site

Dianthus L. (Caryophyllaceae) is a large genus, comprising more than 300 species, and the genus widely occurs in temperate regions of the northern hemi-

sphere (Tutin 1964). In Japan there are four species, of which *D. shinanensis* (Yatabe) Makino is narrowly distributed in the Chubu District, central Honshu of Japan, and *D. superbus* L. is widely distributed throughout Japan (Kitagawa 1982). The former is a biennial herb, while the latter a perennial herb (Shimizu & Umebayashi 1995). They usually open flowers from early July to September, and their flowers are protandrous and secrete nectar from the base of a corolla-tube. The two species share the insect-pollinated floral aspects mentioned just above, but they differ from each other in inflorescence architecture: *D. shinanensis* has flowers cymosely at the uppermost nodes of the shoots (Fig. 1A), while *D. superbus* blooms flowers loosely in cymose inflorescence (Fig. 1B).

To determine the morphospecific differences between the two species and between hermaphrodite and female plants (see Fig. 2), we further examined number of flowers per plant, diameter of corolla, petal length, corolla-tube length (length from the base to the point corresponding to the terminal of calyx-lobes) and ovule number per flower. For measurement of the floral traits several flowers from each plant were collected at natural populations and were

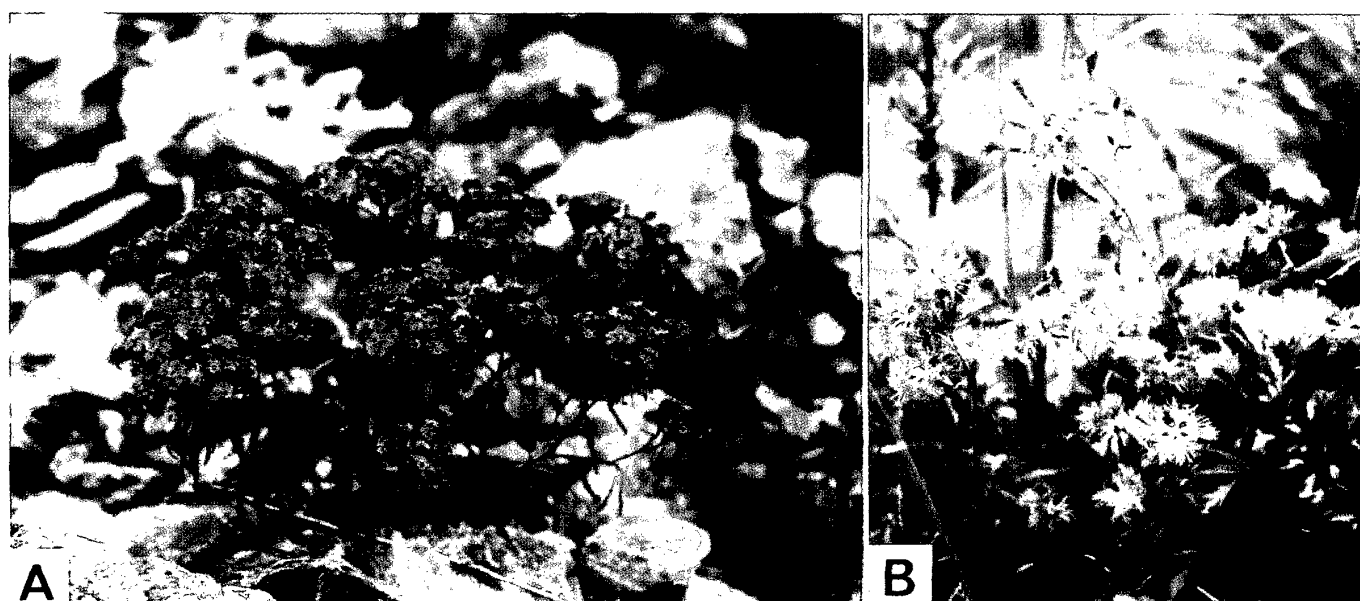


FIG. 1. A: *Dianthus shinanensis* growing on rocky river bed at Hirogawara, Yamanashi Prefecture, and B: *D. superbus* growing in grassland at Hikarijo-yama, Nagano Prefecture.

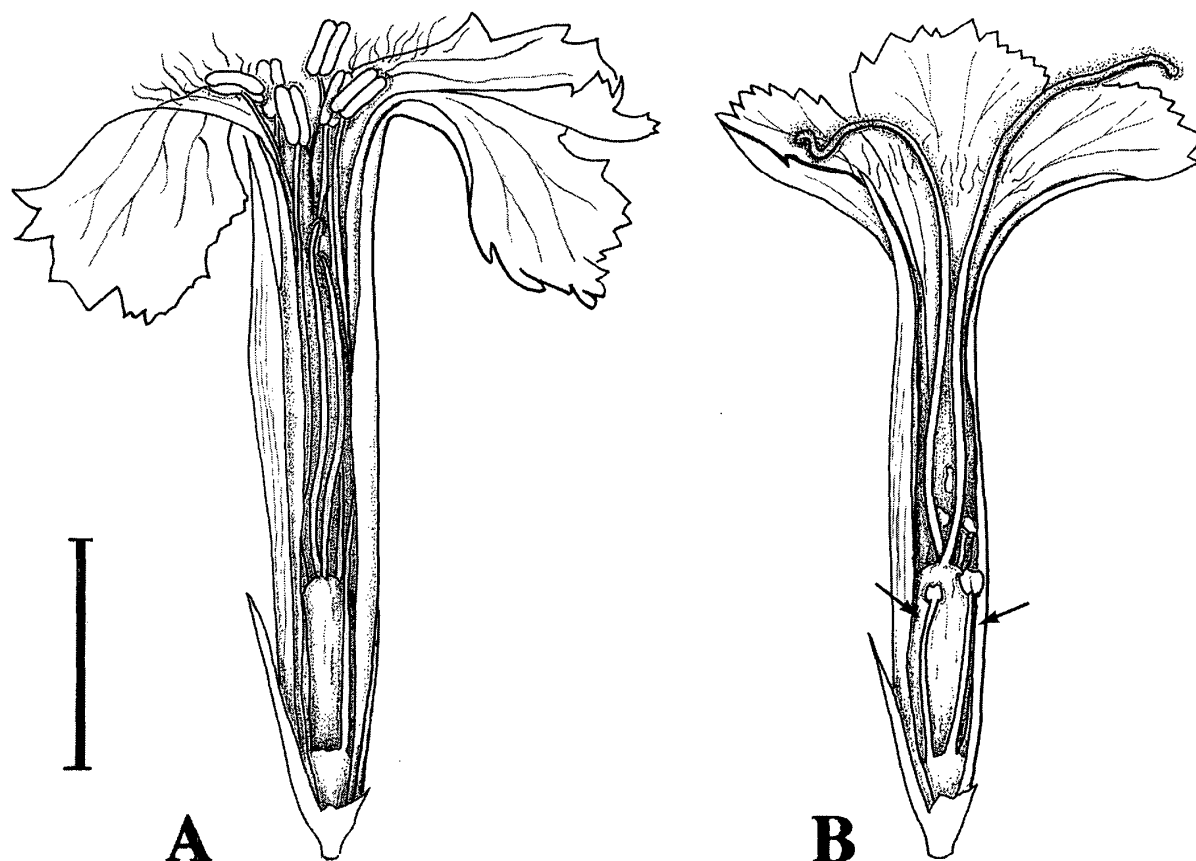


FIG. 2. Hermaphrodite and female flowers of *Dianthus shinanensis*. A: Hermaphrodite flower, showing a male stage. B: Female flower, in which stamens (arrows) are abortive and do not produce pollen grains. Scale bar represents 5mm.

fixed with FAA. After fixation the above floral traits were examined with aid of binocular.

Our study was conducted at two populations for each species. *Dianthus shinanensis* was examined at the two populations located at Hirogawara (HIRO-II), alt. 1900m, and Momonoki (MOMO-I), alt. 900m, in Yamanashi Prefecture. At these localities *D. shinanensis* grew in sunny riverbed. Meanwhile, *D. superbus* was examined at the two populations located at Nagamine (NAGA-I), alt. 900m and Hikarijōyama (HIKARI), alt. 900m, in Nagano Prefecture, where the species grew in sunny grassland dominated by some perennial herbs. The frequencies of the female plants in the study populations are 1.4% (16 female plants, out of the total 1169 plants recorded in 1999) at HIRO-II, 2.3% (18 female plants, out of the total 800 plants recorded in 1999) at MOMO-I, 38.3% (31 female plants, out of the total 81 plants recorded

in 1999) at NAGA-I and 23.7% (23 female plants, out of the total 97 plants recorded in 1999) at HIKARI, respectively. It is notable that the frequency of female plants is remarkably lower in the two populations of *D. shinanensis* than in those of *D. superbus*.

Fruit- and seed-sets and artificial pollination experiments in natural populations

The amounts of fruit-set (matured fruit per flower) and seed-set (matured seed number / ovule number in a fruit) on hermaphrodite and female plants under natural conditions were examined in the two populations (HIRO-II, MOMO-I) of *D. shinanensis* and the two populations (NAGA-I, HIKARI) of *D. superbus*, respectively.

Bagging and artificial self-pollination experiments were carried out to examine the possibility of self-pollination and to confirm the probability of self-

compatibility in flowers of two populations for each species. In this case flower buds were selected randomly in each stem and they were placed in small tea bags (quality of the materials: polyethylene and polypropylene, produced by Marusan Co.) to exclude insect pollinators. After anthesis some of the bagged flowers were left untouched, and the others were artificially self-pollinated and bagged again for a month until fruit maturation. Artificial cross-pollination experiments were also carried out for hermaphrodite and female flowers. In the hermaphrodite flowers, flower buds emasculated were bagged and left untouched for two or three days. After stigma matured (as stigmatic papillae have elongated), the flowers were artificially cross-pollinated and bagged again for a month until fruit maturation.

Flower visitors

Insects visiting hermaphrodite and female plants were observed in the two populations (HIRO-II, MOMO-I) of *D. shinanensis* and the two populations (NAGA-I, HIKARI) of *D. superbus* in summers of 1999. In each population flower visitors were investigated for 10 hours in total. The insects visiting the flowers were recorded and some of them were caught for identification. Their behaviors in flowers were also

observed. In addition, the number of flower visitors per hour was calculated for the two sexual forms of the species. Flower visitation was investigated for 6 hours in the HIRO-II population of *D. shinanensis* and for 7 hours in the NAGA-I population of *D. superbus*, respectively.

Results

Morphological differences between the two species and between the hermaphrodite and female plants

The number of flowers per plant was significantly less in *D. superbus* than in *D. shinanensis*, but the number of ovules per flower was higher in *D. superbus* than in *D. shinanensis* (Table 1). Diameter of corolla and length of petal were smaller in *D. shinanensis* than in *D. superbus* (Table 1). In addition, corolla-tube length of *D. shinanensis* was remarkably shorter than that of *D. superbus*.

In comparison of flowers between hermaphrodite and female plants a notable difference was found in flower size: the hermaphrodite plants produced significantly larger corolla and longer calyx-tube than the female plants in the two species (Fig. 2). In *D. superbus* the number of flowers per plant and the number of ovules per flower did not differ between the her-

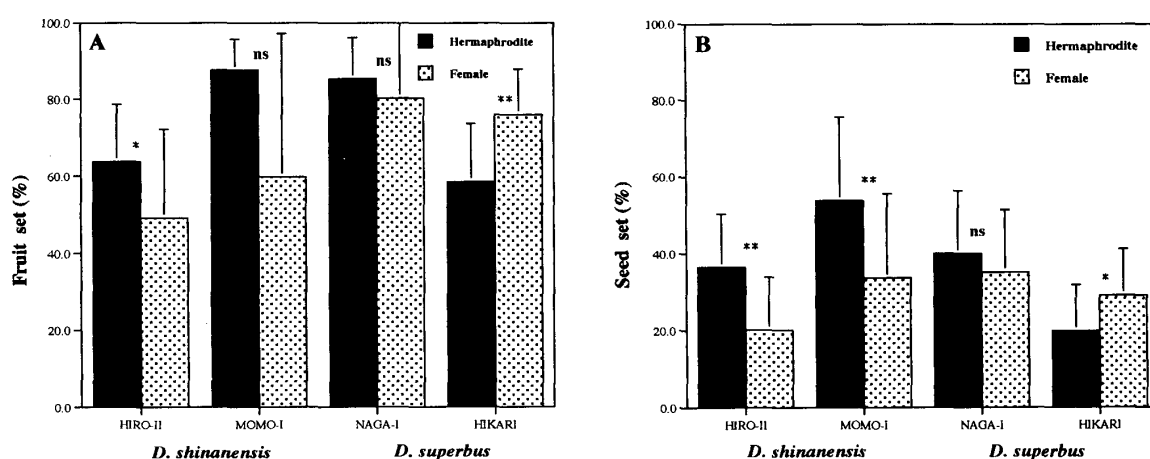


FIG. 3. Fruit and seed set percentages of hermaphrodite and female plants by open pollination in four populations of *Dianthus shinanensis* and *D. superbus*. A: Fruit set percentages of each plant. B: Seed set percentages of each plant. Number of hermaphrodite and female plants examined is 20 and 16 in HIRO-II, 20 and 16 in MOMO-I, 24 and 20 in NAGA-I, 20 and 22 in HIKARI, respectively. Statistic tests (Mann-Whitney's U-test) were carried out between hermaphrodite and female plants within a population. **: $P < 0.01$. *: $P < 0.05$. ns: not significant.

maphrodites and females (Table 1). In *D. shinanensis*, on the other hand, their floral traits are significantly different between the sexual forms: the hermaphrodite plants produce more numerous flowers and ovules than the female plants (Table 1).

Fruit- and seed-sets of hermaphrodites and female plants in natural populations

For *D. shinanensis* average fruit-set percentages by open-pollination were usually higher in hermaphrodite plants than in female plants (Fig. 3A, see also Fig. 4A). The difference was significant between the hermaphrodite and female plants of the HIRO-II population (Fig. 3A). Average seed set percentage was significantly higher in the hermaphrodite plants than in the female plants at the two populations examined of *D. shinanensis* (Fig. 3B). For *D. superbus*, on the other hand, average fruit set percentage was signifi-

cantly higher in female plants than in hermaphrodite plants at the HIKARI population, but was not significant between hermaphrodite plants and female plants at the NAGA-I population (Fig. 3A, see also Fig. 4A). This tendency is identical for seed set percentage of hermaphrodite and female plants of *D. superbus* (Fig. 3B).

Artificial self-pollination and cross-pollination experiments

Bagging experiments showed that no apomixis occurred in the female flowers of the two *Dianthus* species, since none of the bagged female flowers produced fruits and seeds (Fig. 4B, B'). The hermaphrodite flowers of *D. superbus* were able to self-pollinate automatically, since they showed a higher value of fruit set by bagging experiments (69.7% in NAGA-I and 72.4% in HIKARI, see Fig. 4B).

TABLE. 1. Comparison of flower number per plant, diameter of corolla, petal length, calyx-tube length and number of ovules per flower in *D. shinanensis* and *D. superbus*. Statistic test was performed between hermaphrodite and female plants within a population.

Species		Flower number / plant	Diameter of corolla (mm)	Petal length (mm)	Corolla-tube length (mm)	Number of ovules / flower
Study pop.	N	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD
Morph						
<i>D. shinanensis</i>						
HIRO-II						
Hermaphrodite	20	77.0 $\pm$ 50.3	16.8 $\pm$ 1.6	23.1 $\pm$ 1.2	17.3 $\pm$ 1.2	50.9 $\pm$ 6.2
Female	16	42.1 $\pm$ 51.6	11.9 $\pm$ 1.3	19.1 $\pm$ 1.7	15.5 $\pm$ 0.8	43.4 $\pm$ 8.8
Statistic test		p < 0.05 ¹⁾	p < 0.001 ²⁾	p < 0.001 ²⁾	p < 0.001 ²⁾	P < 0.05 ¹⁾
MOMO-I						
Hermaphrodite	20	76.0 $\pm$ 46.3	15.0 $\pm$ 1.5	22.7 $\pm$ 1.3	18.3 $\pm$ 0.6	46.9 $\pm$ 5.9
Female	16	44.7 $\pm$ 35.1	12.3 $\pm$ 1.3	18.4 $\pm$ 1.5	14.9 $\pm$ 1.0	43.4 $\pm$ 3.6
Statistic test		p < 0.05 ¹⁾	p < 0.001 ²⁾	p < 0.001 ²⁾	p < 0.001 ²⁾	P < 0.05 ¹⁾
<i>D. superbus</i>						
NAGA-I						
Hermaphrodite	24	17.8 $\pm$ 15.0	33.3 $\pm$ 5.7	43.4 $\pm$ 3.5	24.6 $\pm$ 1.9	132.4 $\pm$ 17.0
Female	20	17.7 $\pm$ 9.1	23.9 $\pm$ 3.5	34.6 $\pm$ 3.1	23.8 $\pm$ 1.7	127.9 $\pm$ 18.0
Statistic test		p=0.39 ¹⁾	p < 0.001 ²⁾	p < 0.001 ²⁾	p < 0.001 ²⁾	P=0.509 ¹⁾
HIKARI						
Hermaphrodite	20	29.4 $\pm$ 26.2	30.4 $\pm$ 5.5	41.4 $\pm$ 3.6	26.0 $\pm$ 1.5	114.9 $\pm$ 23.9
Female	22	25.4 $\pm$ 31.2	23.3 $\pm$ 3.4	33.1 $\pm$ 2.8	21.7 $\pm$ 2.4	118.4 $\pm$ 20.9
Statistic test		p=0.14 ¹⁾	p < 0.001 ²⁾	p < 0.001 ²⁾	p < 0.001 ²⁾	P=0.399 ¹⁾

¹⁾: Mann-Whitney's U-test. ²⁾: student t-test. N: number of plants examined.

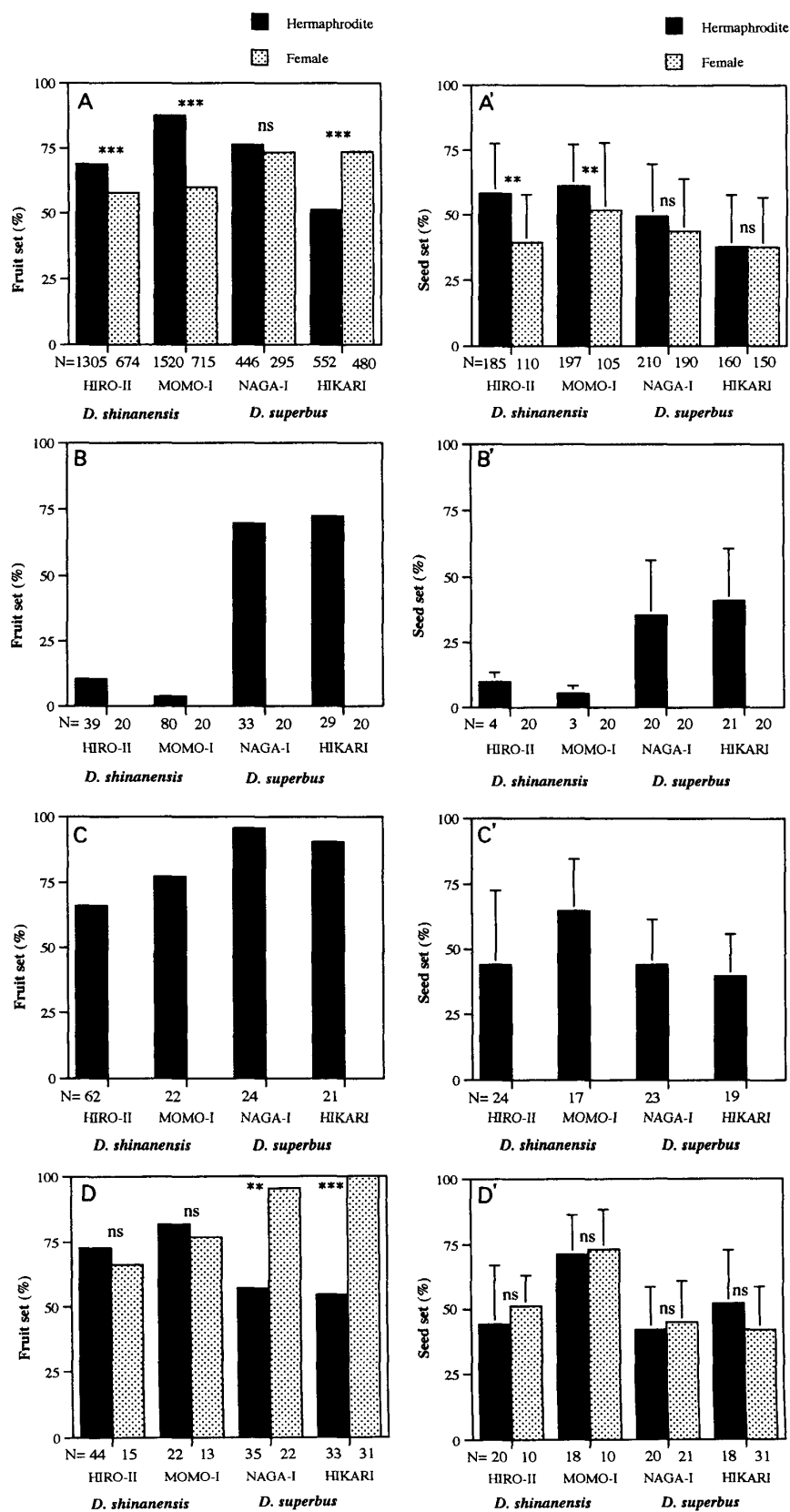


FIG. 4. Fruit and seed set percentages of hermaphrodite and female flowers by artificial pollination experiments in four populations of *Dianthus shinanensis* and *D. superbus*. A, A': control. B, B': bagged. C, C': artificial self-pollination. D, D': artificial cross-pollination. N: number of flowers examined. Statistic tests (Chi Square test for fruit set and Mann-Whitney's U-test for seed set) were carried out between hermaphrodite and female flowers. ***: $P < 0.001$. **: $P < 0.01$. ns: not significant.

Meanwhile, the hermaphrodite flowers of *D. shinanensis* were uneasy to self-pollinate automatically, since their fruit sets by bagging experiments were remarkably lower (10.3% in HIRO-II and 3.8% in MOMO-I, Fig. 4B). Artificial self-pollination experiments showed that the hermaphrodite flowers of two species were self-compatible, and further the fruit set percentages of the hermaphrodite flowers were obviously higher in *D. superbus* (95.7% in NAGA-I and 90.5% in HIKARI) than in *D. shinanensis* (66.1% in HIRO-II and 77.3% in MOMO-I, Fig. 4C, C'). Artificial cross-pollination experiments indicated that the hermaphrodite and female flowers of *D. shinanensis* produced fruits well (Fig. 4D), and they also did not differ significantly from each other in seed-set percentages (Mann Whitney's U-test, $p = 0.350$ in HIRO-II, $p = 0.428$ in MOMO-I, see Fig. 4D'). Although the fruit set percentage of *D. superbus* was significantly higher in female flowers than in hermaphrodite flowers (Fig. 4D), the seed set percentage did not differ significantly between the two different forms ($p = 0.382$ in NAGA-I, $p = 0.079$ in HIKARI, see Fig. 4D').

Flower visitors and frequency of visitations in hermaphrodite and female plants of the two species in natural populations

The insects visiting the flowers of *D. shinanensis* and *D. superbus* were summarized in Table 2, in which the flower visitors were tentatively divided into two groups: one is a group sucking the nectar and the other is a group feeding on pollen grains. Totally, *D. shinanensis* was visited by 19 kinds of insects, some of them sucking the nectar and the others mainly feeding on pollen grains (Table 2). Among them, the two kinds of insects, Sphingidae, Papilionidae and Scarabaeidae, may be ineffective pollinators for the species, since they usually did not touch the *Dianthus* stigmas. On the other hand, *D. superbus* was visited by 6 kinds of insects, most of them sucking the nectar (Table 2). Syrphidae are likely to be less effective as pollinators for *D. superbus*, as they

rarely touched the stigmas of the flowers with their body.

Average frequency of flower visitors per hour was 11.6 in hermaphrodite plants and 4.3 in female plants of *D. shinanensis*, while it was 0.7 in hermaphrodite plants and 0.6 in female plants of *D. superbus* (Table 3). This indicated that the insect pollinators visited more frequently on the flowers of *D. shinanensis*. Furthermore, it can be seen from this table that more frequent visitors are the insects (ex. hover-fly and small bee) feeding on pollen grains for *D. shinanensis* and are the insects (ex. butterfly and bee) sucking nectars for *D. superbus*, respectively (see Table 3).

In terms of the frequency of flower visitors per hour, a significant difference was found between hermaphrodite and female plants of *D. shinanensis* (hermaphrodites, 11.6 times per hour; female, 4.3 times per hour; Mann-Whitney's U-test, $p < 0.05$, Table 3). In the female plants of *D. shinanensis* the hover-flies sometimes flew away without landing on the flowers, and actually the frequency of visiting of the insects feeding on pollen grains (ex. small bee, hover-fly and long-horn beetle) was remarkably reduced. In *D. superbus*, on the other hand, no significant difference was found between the two sexual forms (hermaphrodite, 0.7 times per hour; female 0.6 times per hour; Mann-Whitney's U-test, $p = 0.56$, Table 3).

Discussion

The present results demonstrate that female reproductive success in natural populations markedly differ between *Dianthus shinanensis* and *D. superbus*. In *D. superbus* the female plants produce more numerous seeds than the hermaphrodite plants at the HIKARI population, or produce seeds equal to the hermaphrodite ones at the NAGA-I population. In *D. shinanensis*, on the other hand, the female plants produce significantly less number of seeds than the hermaphrodite plants in the two populations examined. Generally, it is known that the female plants produce

TABLE. 2. Flower visitors in two species of *D. shinanensis* and *D. superbus*.

Species	Flower visitors		Total
	Visitors sucking the nectar	Visitors feeding on pollen grains	
<i>D. shinanensis</i>			
<HIRO-II>	Nymphalidae (2)* <i>Argynnis paphia geisha</i> <i>Inachis io geisha</i> Apidae (1)* <i>Bombus diversus diversus</i> Pieridae (2)* <i>Eurema hecabe mandarina</i> <i>Pieris rapae crucivora</i> Hesperidae (1)* <i>Ochlodes venata herculea</i> Papilionidae (3) <i>Papilio machaon hippocrates</i> <i>Papilio protenor demetrius</i> <i>Papilio biano dehaanii</i> Sphingidae (1) <i>Hemaris radias</i>	Halictidae (1)* <i>Halictus</i> sp. Apidae (1)* <i>Bombus diversus diversus</i> Cerambycidae (1)* <i>Pidonia</i> sp. Syrphidae (3)* <i>Asarkina porcina</i> <i>Betasyrphus serarius</i> <i>Episyphus balteatus</i> Scarabaeidae (1) <i>Blitopertha orientalis</i>	17
<MOMO-I>	Nymphalidae (2)* <i>Argynnis paphia geisha</i> <i>Inachis io geisha</i> Apidae (1)* <i>Bombus diversus diversus</i> Pieridae (2)* <i>Eurema hecabe mandarina</i> <i>Pieris rapae crucivora</i> Hesperidae (1)* <i>Thymelicus leoninus</i> Papilionidae (3) <i>Papilio machaon hippocrates</i> <i>Papilio protenor demetrius</i> <i>Papilio protenor demetrius</i> Sphingidae (1) <i>Hemaris radias</i>	Halictidae (1)* <i>Lasioglossum</i> sp. Apidae (1)* <i>Bombus diversus diversus</i> Syrphidae (3)* <i>Asarkina porcina</i> <i>Betasyrphus serarius</i> <i>Episyphus balteatus</i>	15
<i>D. superbus</i>			
<NAGA-I>	Papilionidae (3)* <i>Papilio machaon hippocrates</i> <i>Papilio protenor demetrius</i> <i>Papilio protenor demetrius</i> Sphingidae (1)* <i>Gurelca himachala sangaica</i>	Pieridae (1)* <i>Eurema hecabe mandarina</i> Syrphidae (1) <i>Shaerophoria menthastris</i>	6
<HIKARI>	Papilionidae (3)* <i>Papilio machaon hippocrates</i> <i>Papilio protenor demetrius</i> <i>Papilio protenor demetrius</i> Sphingidae (1)* <i>Gurelca himachala sangaica</i>	Syrphidae (1) <i>Shaerophoria menthastris</i>	5

*An effective pollinator. Numerals in parenthesis are numbers of species observed.

more numerous seeds than the hermaphrodite plants, or produce seeds equal to the hermaphrodite ones in gynodioecious populations (Delph 1990, Richards 1997, Manicacci *et al.* 1998), as in *D. superbus* pre-

sented here. Unusual condition of seed sets represented by *D. shinanensis* raises the question of why the female reproductive success is lower than the hermaphrodite one in natural populations (see Fig. 3).

TABLE. 3. Frequency of visitation per hour in natural populations of *D. shinanensis* and *D. superbis*. Mean number of open flowers per plant was added in the table.

Species (Pop.)	<i>D. shinanensis</i> (HIRO-II)		<i>D. superbis</i> (NAGA-I)	
Sexual form	Hermaphrodite	Female	Hermaphrodite	Female
Mean number of open flowers per plant	76.5±37.6 (17)	35.0±25.3 (6)	2.9±3.6 (50)	2.6±1.7 (14)
Frequency of visitation per hour	11.6±6.4	4.3±3.4	0.7±0.7	0.6±0.8
< Composition of visitation >				
Large Butterfly (Papilionidae)	-	-	0.4±0.5	0.4±0.5
Middle sized butterfly (Nymphalidae, Hesperidae)	1.8±2.1	0.3±0.8	-	-
Bumblebee (Apidae)	0.1±0.5	0.2±0.4	-	-
Small Bee (Halictidae)	2.9±5.1	1.5±1.8	0.2±0.4	0.1±0.3
Hover-fly (Syrphidae)	5.3±2.9	2.0±2.3	-	-
Long-horn beetle (Cerambycidae)	1.5±2.6	0.3±0.5	-	-

Numerals in parenthesis are number of plants examined.

Throughout the artificial cross pollination experiments, we obtain the result that there is no significant difference in seed set percentage between the female and hermaphrodite flowers (see Fig. 4). Thus it is at least unlikely that seed production of the female plants is limited by the allocation of resources. The female reproductive successes different between the two species may be caused by functions of their different floral morphologies and of their different pollination systems, as being discussed below.

Dianthus shinanensis and *D. superbis* share gross architecture of floral morphology, but they show some differences in floral traits, particularly those related to the pollination system, such as diameter of corolla, petal length, corolla-tube length and number of flowers per stem. *D. shinanensis* has smaller flowers, shorter corolla-tubes and more numerous flowers

per aerial stem, while *D. superbis* has larger flowers, longer corolla-tube and less number of flowers per aerial stem. The floral traits different between the two species develop a pollination system different from each other. As revealed by the present study, *D. shinanensis* is largely pollinated by middle sized-butterflies (Nymphalidae, Pieridae and Hesperidae) sucking nectars secreted from the base of the corolla-tube, and by bees (Halictidae and Apidae) and hoverflies (Syrphidae) feeding on pollen grains exclusively. In contrast, *D. superbis* is mainly pollinated by large sized-butterflies (Papilionidae) and hawkmoths (Sphingidae) with long proboscis, which persistently suck nectars secreted from the base of the corolla-tube.

In natural populations of *Dianthus superbis* no significant difference in frequency of flower visitation

was found between the hermaphrodite and female plants, despite the differences between them in flower size. While in *D. shinanensis* the frequency of flower visitation is markedly lower in the female plants than in the hermaphrodite plants. The female plants of *D. shinanensis* are likely to be less attractive for insect pollinators. Smaller flower size and reduced number of flowers may in part impair the attractiveness of the female plants to the insect pollinators. Of particular importance here is the presence of pollen grains that act as rewards to the insect pollinators. In *D. shinanensis* some of the pollinators (bees and hover-flies) usually visit the flowers to collect pollen grains, and thereby the female flowers lacking pollen grains appear to be less attractive for the pollinators. In *D. superbus*, on the other hand, the effective pollinators largely visit to suck the nectars, and both hermaphrodite and female flowers secrete the nectars from the base of the corolla-tube. Thus no significant difference in the frequency of flower visitation can be found between the two sexual forms. In considering these results, the lower female reproductive success in *D. shinanensis* may be caused by the reduced visits of insect pollinators by lacking pollen rewards, as being reported in a gynodioecious shrub *Hebe stricta* (Delph & Lively 1992).

This study confirms the pollination system and reproductive performance of the two gynodioecious *Dianthus* species. Further question is how the observed lower reproductive success might influence the maintenance of females in natural populations. In order to clarify the above question in future research of *Dianthus* species, further studies will be necessary on the mode of male sterile (female) inheritance and the degree of inbreeding depression that are generally regarded to be important for the maintenance of the female plants (Sakai *et al.* 1997, Manicacci *et al.* 1998).

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